Testing new Pauly Cessational Growth Function

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Introduction

The mean length-at-age for many animals (e.g., CITATIONS) is often modeled with the von Bertalanffy growth function (VBGF; von Bertalanffy (1938)). The parameterization of the VBGF attributable to Beverton and Holt (1957) is most common and may be expressed as

$$L_t = L_\infty(1 - e^{-q}) \qquad (1)$$

with

$$q = K(t - t_0) \qquad (2)$$

where $L(t)$ is the expected or average length at time (or age) t, L_∞ is the asymptotic mean length, K is a measure of the exponential rate of approach to the asymptote (Schnute and Fournier 1980), and t_0 is the theoretical time or age (generally negative) at which the mean length would be zero.

Many animals exhibits seasonal oscillations in growth as a response to seasonal changes in environmental factors such as temperature, light, and food supply (CITATIONS). Equation 2 of the traditional VBGF has been modified, usually with a sin function, to model these seasonal oscillations in growth. The most popular of these modifications is from Hoenig and Choudaray Hanumara (1982) and Somers (1988) (and carefully reiterated in Garcia-Berthou et al. (2012)), and uses

$$\begin{aligned} q = & K(t - t_0) \\ & + \frac{CK}{2\pi} sin(2\pi(t - t_s)) \\ & - \frac{CK}{2\pi} sin(2\pi(t_0 - t_s)) \end{aligned} \qquad (3)$$

where C modulates the amplitude of the growth oscillations and corresponds to the proportional decrease in growth at the depth of the oscillation (i.e., "winter"), and t_s is the time between time 0 and the start of the convex portion of the first sinusoidal growth oscillation (i.e., the inflection point). If C=0, then there is no seasonal oscillation and Equation 3 reduces to Equation 2 and the typical VBGF (Figure 1). If C=1, then growth completely stops once a year at the "winter-point" (WP), whereas values of 0<C<1 result in reduced, but not stopped, growth during the winter (Figure 1).

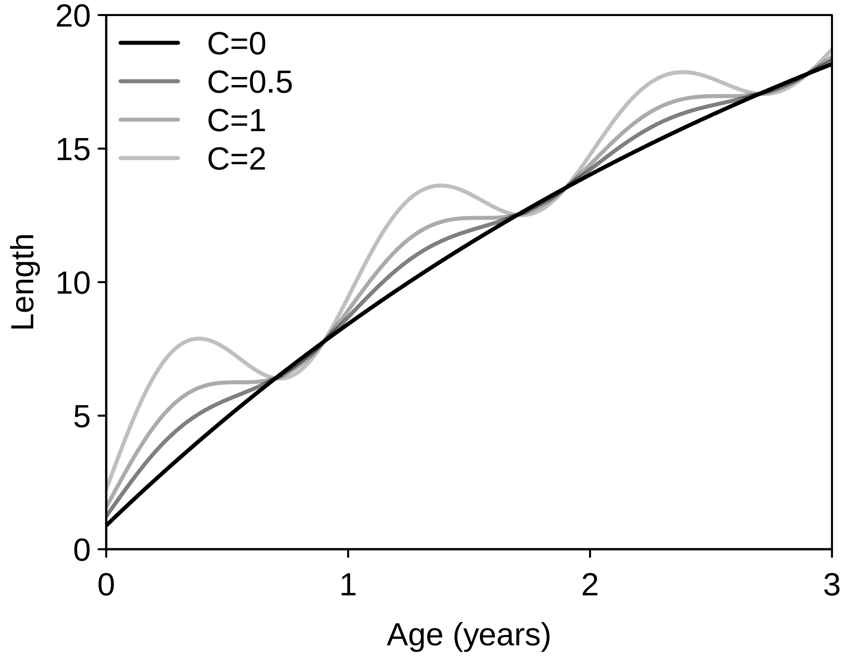


Figure 1: Example VBGF using Equation 3 with L_∞=30, K=0.3, t_0=-0.1, t_s=0.05 (or WP=0.55), and four different values of C.

Values of C>1 (or <0) in Equation 3 allow seasonal decreases in mean length-at-age (Figure 1). A decrease in mean length is unlikely for organisms whose skeletons largely preclude shrinkage (Pauly et al. 1992), although a seasonal decrease in mean length-at-age is possible if size-dependent overwinter mortality occurs (Garcia-Berthou et al. 2012). To address this issue, Pauly et al. (1992) modified Equation 3 to include a true seasonal no-growth period with a smooth transition of the modeled mean length-at-age into and out of the no-growth period. Specifically, their modification is

$$\begin{aligned} q = & K^{'}(t^{'}-t_0) \\ & + \frac{K^{'}(1-NGT)}{2\pi} sin\left(\frac{2\pi}{1-NGT}(t^{'}-t_s)\right) \\ & - \frac{K^{'}(1-NGT)}{2\pi} sin\left(\frac{2\pi}{1-NGT}(t_0-t_s)\right) \end{aligned} \tag{4}$$

where NGT is the "no-growth time" or the length of the no growth period (as a fraction of a year) and $t^{'}$ is found by "subtracting from the real age (t) the total no-growth time occurring up to age t." Furthermore, Pauly et al. (1992) introduced $K^{'}$ to Equation 4 because the units of K change from $year^{-1}$ in Equation 3 to $(1-NGT)^{-1}$ in Equation 4 due to $t^{'}<t$ for any t. We further note that $K^{'}>K$ because annual growth is compressed into a shorter period $(1-NGT)$ in Equation 4 when $NGT>0$.

Pauly et al. (1992) derived Equation 4 by assuming C=1 (i.e., that the rate of growth is 0 at the WP), replacing 2π with $\frac{2\pi}{1-NGT}$ (i.e., restricting the oscillation to the period of growth), and replacing K with $K^{'}$. Their modification can be described geometrically (though not algorithmically) in two steps. First, the seasonal growth function in Equation 3 with C=1 is fit to the observed lengths and ages that have had the cumulative NGT subtracted (i.e., using $t^{'}$). The growth trajectory is then separated at the WP and a horizontal segment that is NGT units long is inserted. This forms a growth trajectory that smoothly transitions into and out of a no-growth period (Figure 2).

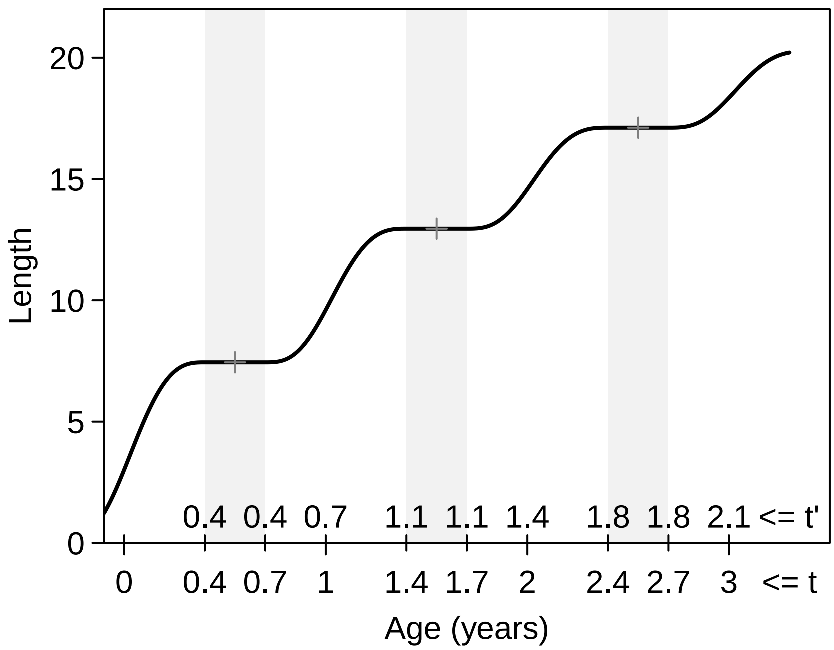


Figure 2: Example VBGF using Equation 4 or Equation 5 with L_∞=30, $K^{'}$=0.4, t_0=-0.1, NGT=0.3, and t_s=0.05 or WP=0.55. Each no-growth period is marked by a light gray polygon and each WP is marked by the gray plus symbol. The ages adjusted for the NGT (i.e., $t^{'}$) are shown above the x-axis.

Pauly et al. (1992) provided a "diskette" that contained a computer program to estimate the parameters of Equation 4. The diskette is difficult (at best) to obtain and the source code is no longer available (D. Pauly, pers. comm.). Pauly et al. (1992) did describe the operations performed by their program, but their is no description of how $t^{'}$ was operationalized. This is an important step in using Equation 4 because $t^{'}$ is a function of t, but it is also a function of NGT and t_s, which are parameters to be estimated during the model-fitting process. In other words, the values for $t^{'}$ will change with each iteration in the non-linear model-fitting process.

The objectives of this note are to (i) describe a function for calculating $t^{'}$ that may be used in the model-fitting process; (ii) describe a slight modification of Equation 4 that eases the calculation of $t^{'}$ while providing a more meaningful parameter; (iii) provide an (open-source) algorithm for the modified function that can be used in model-fitting; and (iv) demonstrate the use of the modified function for fitting length-at-age data.

The Modified Model

The WP value is equal to $t_s + 0.5$ because of the shape of the sin function used to model the growth oscillations. By simple substitution, Equation 4 is modified to include WP rather than t_s.

$$
\begin{aligned}
q = {} & K^{'}(t^{'} - t_0) \\
& + \frac{K^{'}(1-NGT)}{2\pi} sin\left(\frac{2\pi}{1-NGT}(t^{'} - WP - 0.5)\right) \\
& - \frac{K^{'}(1-NGT)}{2\pi} sin\left(\frac{2\pi}{1-NGT}(t_0 - WP - 0.5)\right)
\end{aligned}
\tag{5}
$$

Note that in Equation 5 WP is the center of the no-growth period (Figure 3).

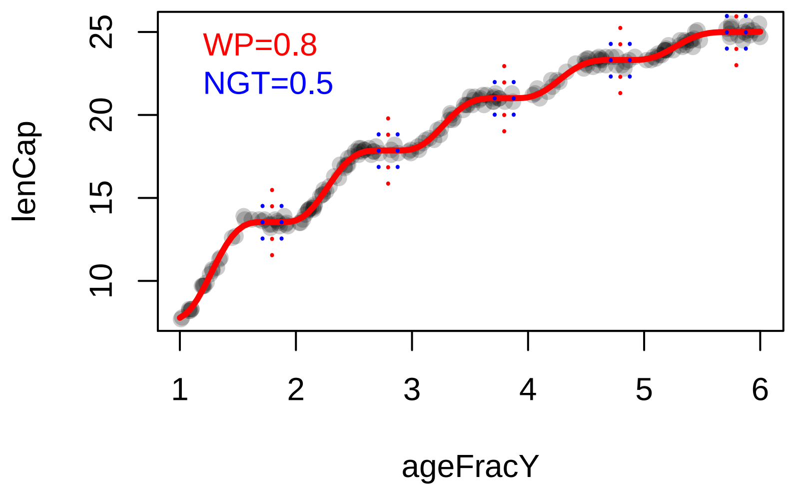
Methods

Simulated Data

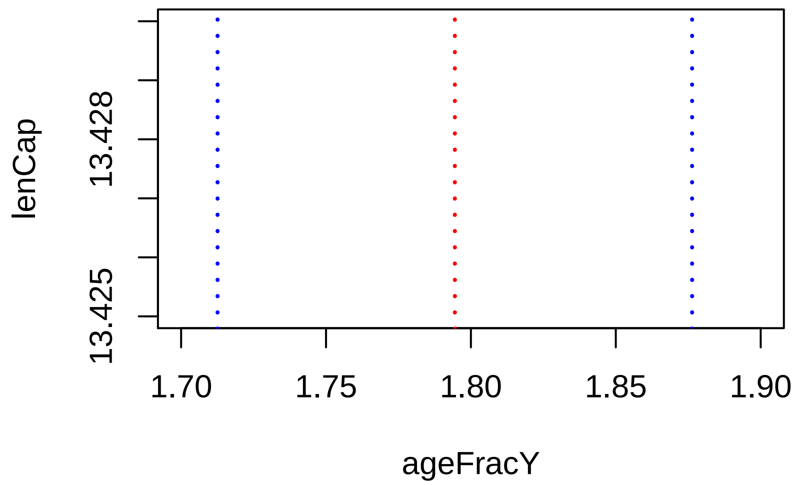
R Implementation

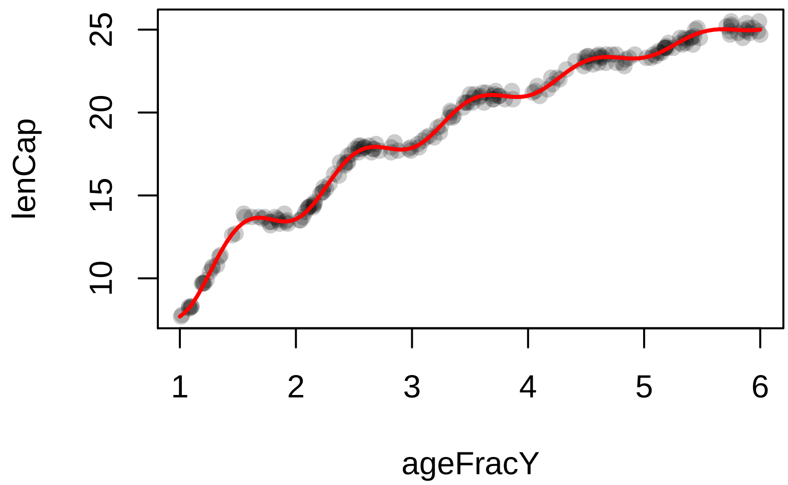
Model Fitting

Simulated Data




```
##              Est       2.5%      97.5%
## Linf 29.5417860 29.2284736 29.8734931
## K     0.3757916  0.3574196  0.3953120
## t0    0.2066147  0.1433949  0.2588665
## WP    0.7944574  0.7850181  0.8039542
## NGT   0.1637617  0.1209022  0.2052301
```






```
##                          2.5%       97.5%
## Linf 29.59794081 29.282403009 29.93253778
## K     0.31220330  0.302209706  0.32223856
## t0    0.04410893  0.002347852  0.07298911
## C     1.31396222  1.233845105  1.39465396
## WP    0.79426117  0.785196437  0.80338659
```

Real Data

Appendix

```
################################################################################
## internal function to compute t-prime
################################################################################
iCalc_tpr <- function(t,WP,NGT) {
  ## No-growth period starts at WP-NGT/2.  Use this to shift each age such that
  ##    first NGT would correspond to a value of 0
  tshift <- WP-NGT/2
  tmp.t <- t-tshift
  ## Find fraction of year on this new time scale for each adjusted age
  ##    by substracting whole number age (e.g, 2.79-2)
  tmp.t2 <- tmp.t-floor(tmp.t)
  ## Adjust this fraction for no growth ... with the time adjustment no-growth
  ##    is from 0 to NGT in each "year" ... tprime will not increase in NGT so
  ##    replace all of these fractions with zeroes.  Above NGT, the tprime must
  ##    have the NGT removed from it (e.g., if NGT=0.4, then 0.79-0.4 is the
  ##    fraction of the year for which growth occurred.)
  for (i in 1:length(tmp.t2)) {
    if (tmp.t2[i]<=NGT) tmp.t2[i] <- 0
    else tmp.t2[i] <- tmp.t2[i]-NGT
  }
  ## Now get the number of completed growth periods (i.e., floor (tmp.t)) times
  ##    the length of a growth period (1-NGT) to get the total growth periods
  ##    completed prior to that year and then add on the fractional piece
  tmp.t <- floor(tmp.t)*(1-NGT)+tmp.t2
  ## Shift back to get tprime (why is NGT needed here)
  tpr <- tmp.t+tshift+NGT
}
```

```
################################################################################
## Main Function
##   Linf, t0 as usual
##   Kpr = K-prime as defined in Pauly et al. (units are diff than usual K)
##   WP = "Winter Period" (middle point of no-growth period)
##      = ts+0.5 (ts from Pauly et al.)
##   NGT = "No Growth Time" = "fraction of a year where no growth occurs"
##   tpr = "t-prime" = actual age (t) minus cumulative NGT prior to t
################################################################################

paulySC <- function(t,Linf,Kpr=NULL,t0=NULL,WP=NULL,NGT=NULL) {
  if (length(Linf)==5) { Kpr <- Linf[[2]]; t0 <- Linf[[3]]
                         WP <- Linf[[4]]; NGT <- Linf[[5]]
                         Linf <- Linf[[1]] }
  tpr <- iCalc_tpr(t,WP,NGT)
  q <- Kpr*(tpr-t0) +
    (Kpr*(1-NGT)/(2*pi))*sin((2*pi)/(1-NGT)*(tpr-WP-0.5)) -
    (Kpr*(1-NGT)/(2*pi))*sin((2*pi)/(1-NGT)*(t0-WP-0.5))
  Linf*(1-exp(-q))
}
```

References

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Pauly, D., M. Soriano-Bartz, J. Moreau, and A. Jarre-Teichmann. 1992. A new model accounting for seasonal cessation of growth in fishes. Australian Journal of Marine and Freshwater Research 43:1151–1156.

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